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THE CYTOLOGY OF THE GENUS *HAEMANTHUS* L. (AMARYLLIDACEAE)

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Abstract

A cytological survey of fifteen species and five subspecies of the genus *Haemanthus*, using conventional staining as well as Quinacrine fluorescence and C-banding techniques, has confirmed its chromosome number uniformity: all the species have a chromosome complement of $2n = 2x = 16$. Chromosome rearrangements, including translocations and pericentric inversions, allow the species to be subdivided into two discrete Groups with three Sections each. Overall chromosome differentiation between the species conforms with the conventional taxonomy of the genus. Two species, *H. albiflos* and *H. strigosus* (*H. humilis* complex) have been found to possess two distinct chromosome races. In the case of *H. albiflos* a spontaneous hybrid between its two races is described. Two species, *H. coccineus* and *H. unifoliatus*, have B-chromosomes.

Uittreksel

DIE SITOLOGIE VAN DIE GENUS *HAEMANTHUS* L. (AMARYLLIDACEAE)

'n Sitologiese opname van vyftien species en vyf subspecies van die genus *Haemanthus* waarvoor konvensionele kleurtegnieke sowel as kienakrien-fluoressensie en C-band tegnieke gebruik is, het bevestig dat die chromosoomgetal eenvormig is: al die species het 'n chromosoomgetal van $2n = 2x = 16$. Dit is moontlik om die species in twee groepe met drie seksies elk te verdeel deur van chromosoomherrangskikkings, wat translokasie en perisentriese omkerings insluit, gebruik te maak. Algemene chromosoomdifferensiasie tussen die species stem ooreen met konvensionele taksonomie van die genus. Twee species, *H. albiflos* en *H. strigosus* (*H. humilis* kompleks) blyk twee onderskeie chromosoomrasse te hê. In die geval van *H. albiflos* word 'n spontane kruising tussen die twee rasse beskryf. Twee species, *H. coccineus* en *H. unifoliatus*, het B-chromosome.

Key words: *Haemanthus*, chromosome evolution, taxonomy.

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INTRODUCTION

A chromosome study of nine species of *Haemanthus* has been recently published (Vosa & Marchi, 1980). The present paper presents the cytological analysis of fifteen species and five subspecies out of the twenty-six taxa so far recognised in the genus. It is presented in conjunction with the most recent taxonomic survey (Snijman, 1984) and includes chromosome studies of all the species under cultivation, together with a discussion on chromosome evolution within the genus.

MATERIAL AND METHODS

All the species used in the present study were collected in the wild. Collection data are indicated in Table 1.

For the cytological preparation generally, actively growing root-tips were pretreated with an aqueous solution of colchicine (0,05 %) for 4–5 hours at room temperature. After pretreating and in order to avoid chromosome "bubbling", the root-tips were washed in distilled water, dried quickly on filter paper and placed in 1 : 3 acetic-alcohol for a half-hour. The root-tips were then removed, dried again on filter paper and placed in fresh fixative overnight.

Staining was performed in Feulgen. C-banding and Quinacrine fluorescence staining methods were those used by Vosa (1973).

The haploid ideograms were prepared with measurements taken with camera lucida on at least five mitotic metaphases for each species, on several individuals where possible. Care was taken to choose equally contracted chromosomes in all cases.

In the ideograms the chromosomes are arranged in sequence according to decreasing length from left to right.

Small secondary constrictions are often visible in some of the chromosomes: in the drawings they are indicated by broken lines.

Micrographs were taken on permanent preparations with a Zeiss Ultraphot II microscope using REKORDAK AHU microfilm (Kodak).

In all micrographs the bar represents 10 μ.

RESULTS AND DISCUSSIONS

The results of this investigation confirm the earlier findings that the genus *Haemanthus* is chromosomally uniform.

One of its characteristics is the very large chromosomes and the absence of heterochromatic blocks (Vosa & Marchi, 1980). There are no chromocentres in the interphase nuclei and C-banding produces only very thin bands adjacent to the nucleolar attachments.

TABLE 1

Collection data of *Haemanthus* species.

Species	Collector's name and number	
1. *humilis* Jacq. subsp. *hirsutus* (Baker) Snijman	Matthews 886	(OXF)
,, ,, ,, ,, ,, ,,	Matthews 894	(NBG)
,, ,, ,, ,, ,, ,,	Matthews 933	(NBG)
,, ,, ,, ,, ,, ,,	Matthews 1015	(NBG)
2. *montanus* Baker	Lavranos s.n.	(OXF)
3. *crispus* Snijman	Hardick sub NBG 889/71	(NBG)
,, ,,	Snijman 428	(NBG)
4. *strigosus* Herbert *(humilis* Jacq. subsp. *humilis)*		
,, ,, (A)	Batten 591	(NBG)
,, ,, (A)	Vosa 2059	(OXF)
,, ,, (A)	Vosa 2056	(OXF)
,, ,, (B)	Snijman 471	(NBG, OXF)
5. *barkerae* Snijman	Hiemstra & Hardick sub NBG 899/71	(NBG)
,, ,,	Snijman 96	(NBG)
6. *namaquensis* R. A. Dyer	Snijman 159	(NBG)
7. *albiflos* Jacq. ST5	Roux 307	(NBG)
,, ,, SM5	Roux 90	(NBG)
,, ,, ST5	Snijman 468	(NBG)
,, ,, SM5	Snijman 492	(NBG)
,, ,, ST5	van Jaarsveld 6834	(OXF)
,, ,, SM5	van Jaarsveld 6844	(OXF)
,, ,, SM5	van Jaarsveld 6908	(OXF)
,, ,, ST5	van Jaarsveld 6913	(OXF)
,, ,, ST5 × SM5	Vosa 381/79	(OXF)
,, ,, ST5	Vosa 1477	(OXF)
,, ,, ST5	Vosa 1497	(OXF)
,, ,, SM5	Vosa 1519	(OXF)
,, ,, ST5	Vosa 2160	(OXF)
,, ,, SM5	Vosa 2181	(OXF)
,, ,, ST5	Vosa 2202	(OXF)
,, ,, ST5	Vosa 2205	(OXF)
,, ,, SM5	Vosa 2056	(OXF)
8. *sanguineus* Jacq.	Moriarty 321	(NBG)
,, ,,	Rourke 1665	(NBG)
,, ,,	Snijman 95	(NBG)
9. *canaliculatus* Levyns	van Essen s.n.	(NBG)
10. *pumilio* Jacq.	Olivier 152	(NBG)
,, ,,	Snijman 248	(NBG)
11. *lanceifolius* Jacq.	Snijman 147	(NBG)

12. *amarylloides* Jacq. subsp. *amarylloides*	Snijman 599	(NBG)
,, ,, ,, *polyanthus* Snijman	Snijman 415	(NBG)
,, ,, ,, *toximontanus* Snijman	Olivier 193	(NBG)
13. *graniticus* Snijman	Snijman 424	(NBG)
14. *coccineus* L.	Hiemstra 120	(NBG)
,,	Snijman 3	(NBG)
,,	Stayner sub NBG 1026/71	(NBG)
15. *unifoliatus* Snijman	du Plessis 417	(NBG)
,, ,,	Snijman 158	(NBG)
16. *pubescens* L.f. subsp.*pubescens*	Snijman 89	(NBG)
,, ,, ,, *leipoldtii* Snijman	Snijman 430	(NBG)
,, ,, ,, *arenicolus* Snijman	van Berkel 313	(NBG)

TABLE 2

Previous chromosome counts in the genus *Haemanthus*

Species	$2n =$	Author and year
albiflos Jacq.	16	Inariyama, 1937; Sato, 1938, 1942; Tjio and Levan, 1950; Bjørnstad and Friis, 1972; Vosa and Marchi, 1980.
,, ,, (as *albiflorus**)	16	Heitz, 1926.
,, ,, (as *albomaculatus* Baker)	16	Vosa and Marchi, 1980.
montanus Baker (as *amarylloides* Jacq.)	16	Brighton (quoted by Bjørnstad and Friis, 1972).
carneus Ker Gawler	16	Vosa and Marchi, 1980.
coccineus L.	16	Inariyama, 1937; Sato, 1938, 1942; Bjørnstad and Friis, 1972; Vosa and Marchi, 1980.
,, ,, var. *coarctatus* Baker	16	Heitz, 1926.
,, ,, (as *hyalocarpus* Jacq.)	16	Vosa and Marchi, 1980.
,, ,, (as *tigrinus* Jacq.)	16	Gouws, 1964; Vosa and Marchi, 1980.
*fimbriatus**	16	Heitz, 1926.
humilis Jacq. (as *hirsutus* Baker)	16	Gouws, 1949.
,, ,, (as *nelsonii* Baker)	16	Gouws, 1949; Vosa and Marchi, 1980.
pubescens L.f.	16	Vosa and Marchi, 1980.
,, ,, var. *hirsutus**	16	Heitz, 1926.
sanguineus Jacq. (as *rotundifolius* Ker Gawler)	16	Vosa and Marchi, 1980.

**nomina nuda*

With Quinacrine staining the chromosomes of *Haemanthus* fluoresce evenly along their length.

All the species so far investigated have a chromosome number of $2n = 16$ and a bimodal karyotype consisting of five or six pairs of large chromosomes (L) and three or two pairs of small chromosomes (S).

Previous chromosome counts in the genus are indicated in Table 2.

It has been shown that *Haemanthus* originated from the allied and less specialised genus *Scadoxus*, by a chromosome translocation which resulted in the disploid reduction of the chromosome number from $2n = 18$ to $2n = 16$ (Vosa & Marchi, 1980, and Fig. 1).

On the basis of chromosome analysis, the twenty taxa studied can be subdivided into two discrete Groups, *L*- and *S*-. The denominations *L*- and *S*- refer to the possession of a longer short-arm or a shorter short-arm of chromosome 1, respectively (Fig. 1 and Table 5).

Group *L*- includes seventeen taxa where chromosome 1 is submedian with an arm ratio from about 2,0 to 2,7 and Group *S*- includes four species where chromosome 1 is subterminal with an arm ratio of about 4,8 to 6,5 (Tables 3 and 4).

The mutation responsible for the change in arm ratio of chromosome 1 involves the translocation of a relatively large segment between the short arm of chromosome 1 and the long arm of chromosome 6 (Figs 1 and 2).

Taking into account significant chromosome rearrangements, the two Groups can be further subdivided into three Sections each (Fig. 1 and Table 5).

In all the species the nucleolar organiser, in the form of a small trabant, is always distally located. It may be found in the short-arm or sometimes in the long-arm and in most cases in the largest chromosomes of the complement. It is usually found in a heterozygous condition and its location is variable even within the same species (Vosa & Marchi, l.c.). In the ideograms its position is indicated by a small circle.

In the course of the present study a population of a race of *H. albiflos* (race ST5, see below) was found to be chromosomally heterogeneous. Of nine individuals analysed, three had nucleolar attachments in the short-arm of chromosome 1, two had nucleolar attachments in the long-arm of chromosome 5, and in the remaining three the nucleolar attachments were present in both chromosomes. In all individuals the nucleolar attachments were in a heteromorphic condition.

The chromosome situation in *H. albiflos* presents special problems. The species is widespread along the eastern coast of southern Africa. Two distinct chromosome races are present: one which is indistinguishable from Section *L*-1 (race SM5 = submedian chromosome 5, Figs 7a and 12n) and one which represents Section *L*-3 (race ST5 = subterminal chromosome 5, Figs 1d, 8a and 13c).

Table 3

Chromosome measurements in μ, arm ratio and type of the haploid complement of three species of *Haemanthus* (Group *L*-).

Haemanthus pumilio [*L*-1]

	1	2	3	4	5	6	7	8	Totals
S	6,75	2,90	1,60	2,50	3,40	1,80	2,50	1,80	23,25
L	13,95	13,50	13,70	9,20	7,65	4,45	2,70	2,65	67,80
Totals	20,70	16,40	15,30	11,70	11,05	6,25	5,20	4,45	91,05
S/L	2,06	4,65	8,56	3,68	2,25	2,47	1,08	1,47	
Type	sm	st	t	st	sm	sm	m	m	

Haemanthus amarylloides subsp. *amarylloides* [*L*-2]

	1	2	3	4	5	6	7	8	Totals
S	5,40	2,50	1,30	2,50	1,10	2,00	2,50	1,80	19,10
L	14,70	14,20	13,70	9,90	8,10	4,50	2,70	3,00	70,80
Totals	20,10	16,70	15,00	12,40	9,20	6,50	5,20	4,80	89,90
S/L	2,72	5,68	10,50	3,96	7,36	2,25	1,08	1,60	
Type	sm	st	t	st	t	sm	m	m	

Haemanthus albiflos ST5 [*L*-3]

	1	2	3	4	5	6	7	8	Totals
S	5,60	2,25	1,10	2,30	0,70	2,70	1,35	1,80	17,80
L	14,20	14,15	13,50	10,35	7,90	5,30	3,80	3,00	72,20
Totals	19,80	16,40	14,60	12,65	8,60	8,00	5,15	4,80	90,00
S/L	2,53	6,28	12,27	4,50	11,28	1,96	2,81	1,66	
Type	sm	st	t	st	t	sm	sm	m	

TABLE 4

Chromosome measurements in μ, arm ratio and type of the haploid complement of three species of *Haemanthus* (Group *S*-).

Haemanthus crispus [*S*-1]

	1	2	3	4	5	6	7	8	Totals
S	2,10	1,95	1,15	1,85	3,25	3,00	1,40	1,50	16,20
L	13,70	12,55	12,80	10,30	8,40	6,95	4,40	2,80	71,90
Totals	15,80	14,50	13,95	12,15	11,65	9,95	5,80	4,30	88,10
S/L	6,52	6,43	11,13	5,56	2,58	2,31	3,14	1,86	
Types	st	st	t	st	sm	sm	st	sm	

Haemanthus barkerae [*S*-2]

	1	2	3	4	5	6	7	8	Totals
S	2,35	2,25	1,45	2,65	3,80	1,70	1,65	2,05	17,90
L	13,80	12,35	12,95	10,30	8,80	6,45	4,40	2,95	72,00
Totals	16,15	14,60	14,40	12,95	12,60	8,15	6,05	5,00	89,90
S/L	5,87	5,48	8,93	3,88	2,31	3,79	2,66	1,43	
Types	st	st	t	st	sm	st	sm	m	

Haemanthus namaquensis [*S*-3]

	1	2	3	4	5	6	7	8	Totals
S	2,75	1,70	1,40	2,65	3,25	3,85	1,65	1,70	18,95
L	13,30	12,90	12,35	10,45	8,15	5,75	4,10	2,75	69,85
Totals	16,05	14,60	13,75	13,10	11,50	9,60	5,75	4,45	88,80
S/L	4,83	7,58	8,82	3,94	2,53	1,49	2,48	1,61	
Types	st	t	t	st	sm	m	sm	m	

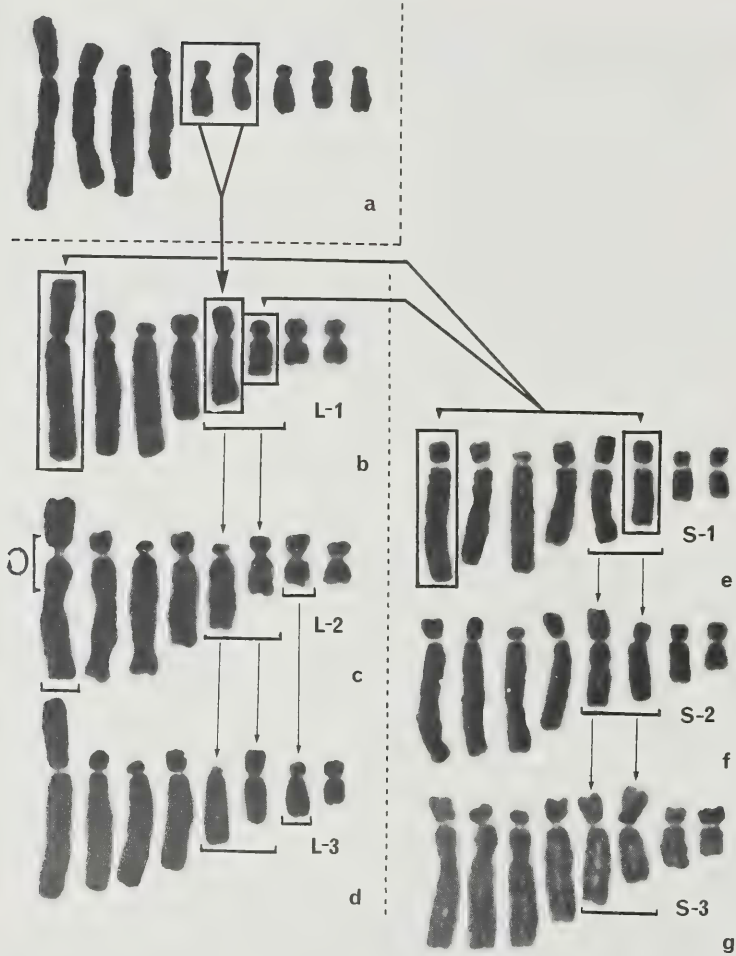

FIG. 1.
The chromosome relationship between *Scadoxus* and *Haemanthus* and within *Haemanthus*, between its two Groups and six Sections. The main chromosomal rearrangements responsible for the differentiation between *Scadoxus* and *Haemanthus* (see Vosa and Marchi, 1980) and between the two Groups of species in *Haemanthus* are indicated by boxing and connected by heavy lines and arrows. The rearrangements between the Sections (within the Groups) by underlining. The small arrows show the probable sequences of rearrangements. a, Haploid complement of *Scadoxus puniceus*; b. *Haemanthus pumilio* [*L*-1]; c. *H. amaryllоides* subsp. *amaryllоides* (*L*-2); d. *H. albiflos* ST5 [*L*-3]; e. *H. crispus* [*S*-1]; f. *H. barkerae* [*S*-2]; g. *H. namaquensis* [*S*-3].

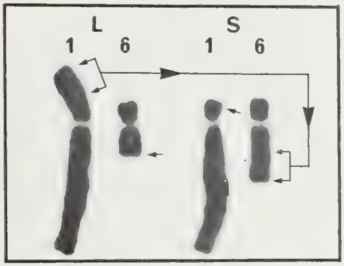

FIG. 2.
Reconstruction of the assumed translocation between chromosome 1 and 6 in *Haemanthus*, responsible for the splitting of the genus into the *L*- and the *S*-Groups. The arrows and the lines indicate the points of breakage and reunion and the direction of the translocation.

Sixteen collections have been analysed and no obvious geographical or ecological correlation has been found.

The proportion of the two races in the sixteen collections is about equal with nine of race ST5 and seven of race SM5.

Overall the two races are morphologically similar. However, under cool greenhouse conditions, race ST5 flowers earlier in the year and more regularly than race SM5.

It is probable that we are witnessing here one of the first events in speciation, where two races of the same species, though still phenotypically similar, have already begun to diverge genetically.

One plant of *H. albiflos* from the Bloukrans area, near Grahamstown, has proved to be a hybrid between the two chromosome races. Morphologically it is indistinguishable from typical *H. albifos* sens. lat. It grows well under ordinary cool greenhouse conditions, but it rarely flowers. Its chromosome complement is illustrated in Figs 11a and 11b.

One plant of *H. canaliculatus* has been found to have a translocation between chromosomes 2 and 3. This is present in heterozygous conditions and is illustrated in Figs 10a and 10b.

B-chromosomes have been found in only two species, *H. coccineus*, in one plant collected at the foot of Jonas Kop (3319-CD: Worcester) illustrated in Fig. 5c, and in a plant of *H. unifoliatus*, collected SW of Steinkopf (2917-BC: Springbok). In both species they are very small and telocentric.

Their existence in two distinct species, far apart geographically, and their identity in size and shape, points to their great antiquity in the phylogeny of the genus.

Table 5
Chromosome Classification of the Genus *Haemanthus*

GROUP *L*-
Section 1
- *humilis* subsp. *hirsutus*
- *montanus*
- *sanguineus*
- *canaliculatus*
- *pumilio*
- *lanceifolius*
- *amarylloides* subsp. *polyanthus*
- *amarylloides* subsp. *toximontanus*
- *graniticus*
- *coccineus*
- *unifoliatus*
- *pubescens* subsp. *pubescens*
- *pubescens* subsp. *leipoldtii*
- *albiflos* SM5
- *strigosus* B *(humilis* subsp. *humilis)*

Section 2
- *amarylloides* subsp. *amarylloides*
- *pubescens* subsp. *arenicolus*

Section 3
- *albiflos* ST5

GROUP S-
Section 1
- *crispus*
- *strigosus* A *(humilis* subsp. *humilis)*

Section 2
- *barkerae*

Section 3
- *namaquensis*

Description of the Karyotypes

Mitotic metaphases and diagrammatic representations of the haploid karyotypes of all the species are illustrated in Figs 3 to 13.

Group L: for the purpose of comparison, Section *L*-1, the largest of the Group, with fifteen taxa (see Table 5), is taken as basic (Fig. 1b; Figs 3a, b, c; 4a, b, c; 5a, b, c; 6a, b, c; 7a; 10a; 12a to 12n).

Section *L*-2 includes two taxa, *H. pubescens* subsp. *arenicolus* and *H. amarylloides* subsp. *amarylloides*. It differs from Section *L*-1 in the interchange between a segment of the short-arm of chromosomes 5 and 6 and in the probable pericentric inversion of chromosome 1 (Figs 1c, 7b, 7c, 13a and 13b).

Section *L*-3 includes the ST5 race of *H. albiflos*. It differs from Section *L*-1 in a probable complex interchange between chromosomes 5 and 6 resulting in the change from submedian to subterminal and from subterminal to submedian, respectively, and in the pericentric inversion of chromosome 7 (Figs 1d, 8a and 13c).

Group S: for the purpose of comparison Section *S*-1 is taken as basic. It includes two species, *H. crispus* and race A of *H. strigosus* (see below), and their mitotic chromosomes and basic karyotypes are illustrated in Figs 1e, 8b, 8c, 13d and 13e.

In the taxonomic treatment *H. strigosus* has been placed within *H. humilis* complex (Snijman, 1984).

Four collections have been analysed, three *(Batten 591; Vosa 2059* and *2056)* have a chromosome complement which belongs to the *S*-Group, Section 1, together with *H. crispus*. These three collections are indicated by the letter A in Table 1. The karyotype of the other collection, *Snijman 471*, belongs to the *L*-Group, Section 1, and is indicated by the letter B in Table 1.

The *H. humilis* complex is very polymorphic and detailed studies on more extensive field collections are needed to clarify the situation. For a discussion of the taxonomic problems in this complex see the taxonomic treatment (Snijman, 1984).

Section *S*-2 includes *H. barkerae*, and differs from Section *S*-1 in a pericentric inversion which has altered the morphology of chromosome 5 from submedian to median (Figs 1f, 9a and 13f).

Section *S*-3 includes *H. namaquensis* and differs from Section *S*-1 in a complex interchange and possible inversion which has altered the morphology of chromosomes 5 and 6 (Figs 1g, 9b and 13g).

The presence of a similar chromosome 1 in *Scadoxus* and in the *L*-Group of *Haemanthus* is an indication that this Group is the most primitive.

It is interesting to note that only chromosomes 1, 4, 5 and 6 are involved in the major rearrangements resulting in the differentiation in both Groups of *Haemanthus* and, indeed, chromosome 6 in the origin of *Haemanthus* itself from a *Scadoxus* ancestor (Figs 1a and 1b and see Vosa & Marchi, l.c.).

Further, the observation of a small secondary constriction in the short-arm of chromosome 1 in some of the *L*-Group species (Figs 3a, 3b, 3c, 4a, 12a, 12b, 12c and 12e), in a position more or less corresponding with the translocation break-point, resulting in the *L*- to *S*-Group differentiation, may be an indication of a structural predisposition to breakage.

It is possible, in fact, to speculate that there exists a genetically controlled variability in this group of chromosomes resulting in the discontinuities on which the selective forces work and is responsible for speciation.

Chromosome measurements, taken on one species for each Section in the two Groups (Tables 3 and 4), show very well their differences as well as their obvious similarities. In particular, the total chromosome length of the haploid karyotypes is shown to vary very little. Taking into account some probable small deletions and/or duplications, it is remarkably uniform for the genus, in spite of the relatively large chromosome rearrangements.

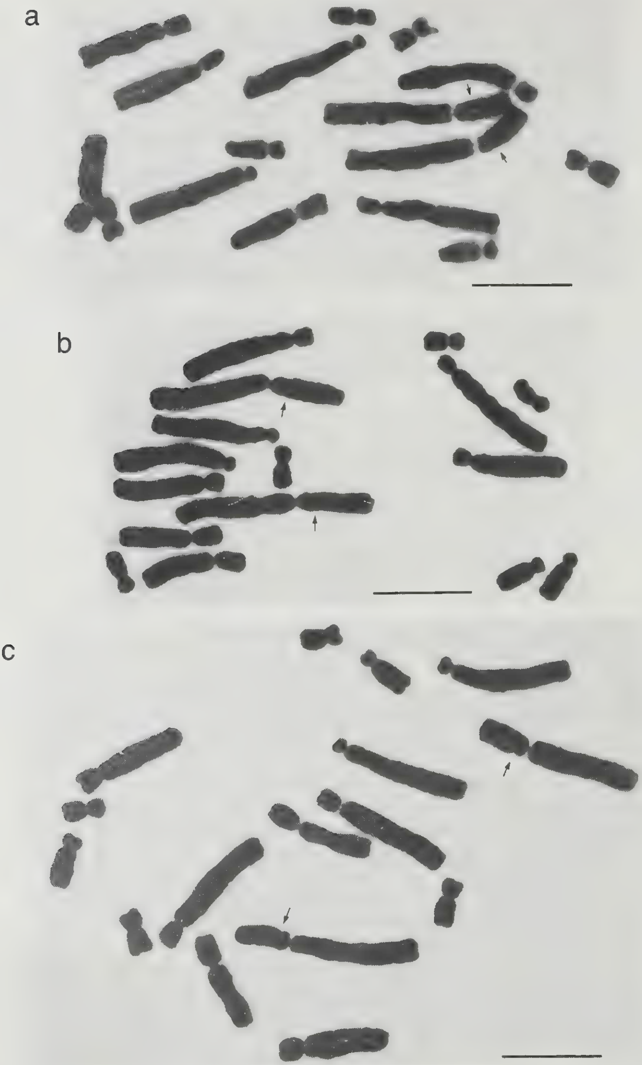

Fig. 3.

a. Mitotic metaphase in *H. humilis* subsp. *hirsutus* [*L*-1]. Note the secondary constriction in the short-arm of chromosome 1, indicated by arrows; b. Mitotic metaphase in *H. montanus* [*L*-1]. Note the secondary constriction in the short-arm of chromosome 1, indicated by arrows; c. Mitotic metaphase in *H. sanguineus* [*L*-1]. Note the secondary constriction in the short-arm of chromosome 1, indicated by arrows.

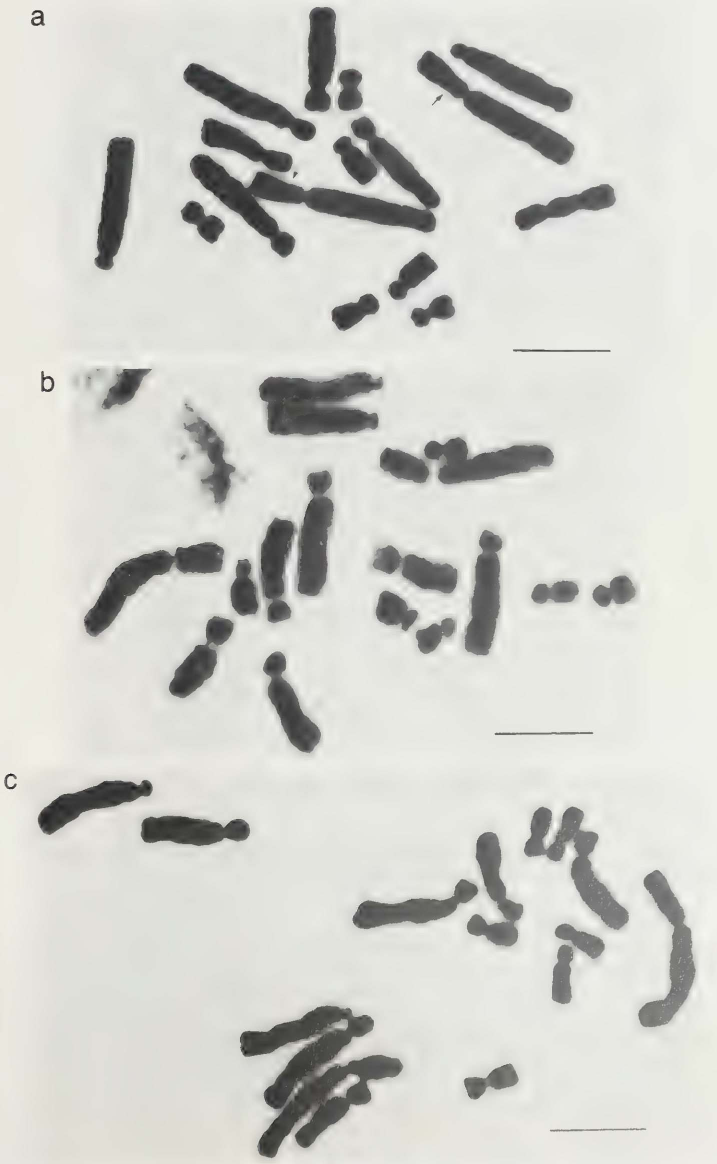

FIG. 4.
a. Mitotic metaphase in *H. pumilio* [*L*-1]. Note the secondary constriction in the short-arm of chromosome 1, indicated by arrows; b. *H. lanceifolius* [*L*-1]; c. *H. amarylloides* subsp. *polyanthus* [*L*-1].

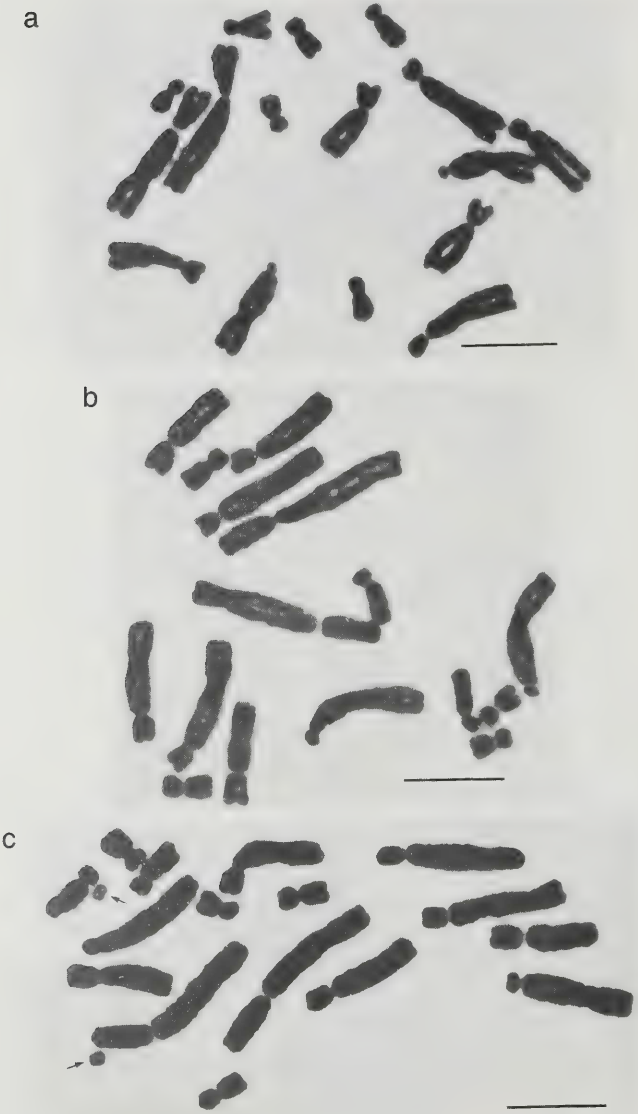

Fig. 5.

a. Mitotic metaphase in *H. amarylloides* subsp. *toximontanus* [*L*-1]; b. *H. graniticus* [*L*-1]; c. *H. coccineus* [*L*-1]. Note telocentric B-chromosomes (arrows).

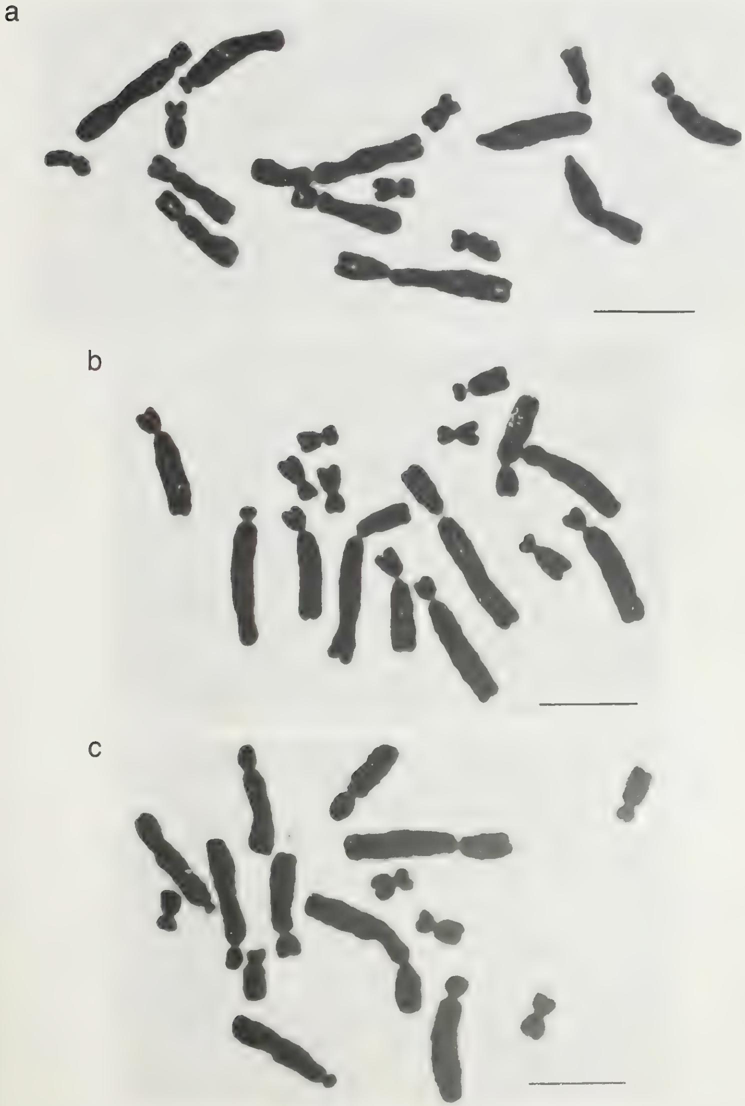

FIG. 6.
a. Mitotic metaphase in *H. unifoliatus* [*L*-1]; b. *H. pubescens* subsp. *pubescens* [*L*-1]; c. *H. pubescens* subsp. *leipoldtii* [*L*-1].

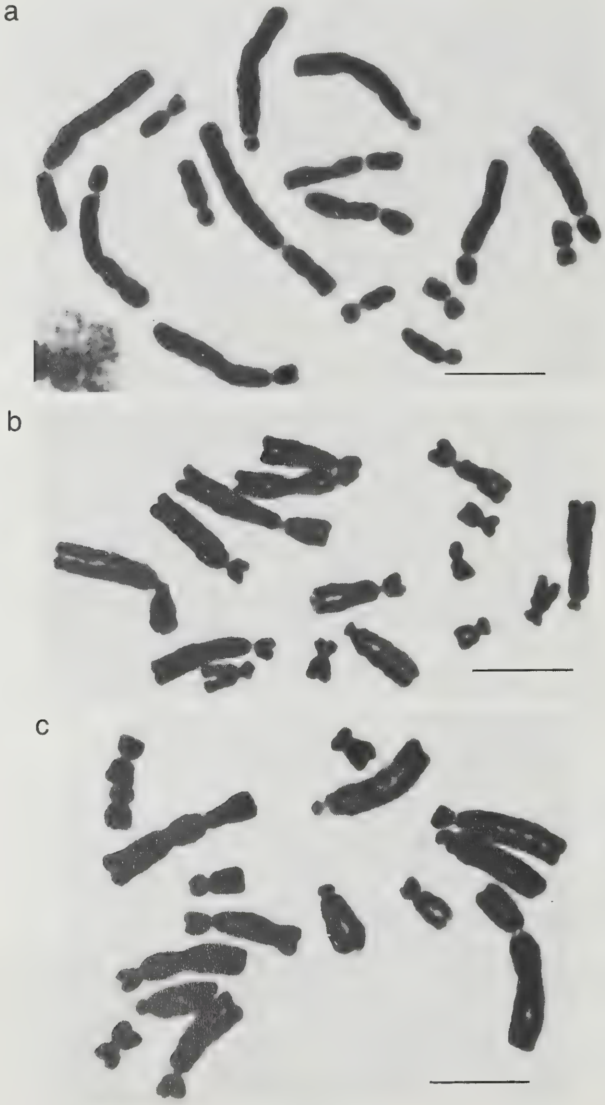

FIG. 7.
a. Mitotic metaphase in the race SM5 of *H. albiflos* [*L*-1]; b. *H. amarylloides* subsp. *amarylloides* [*L*-2]; c. *H. pubescens* subsp. *arenicolus* [*L*-2].

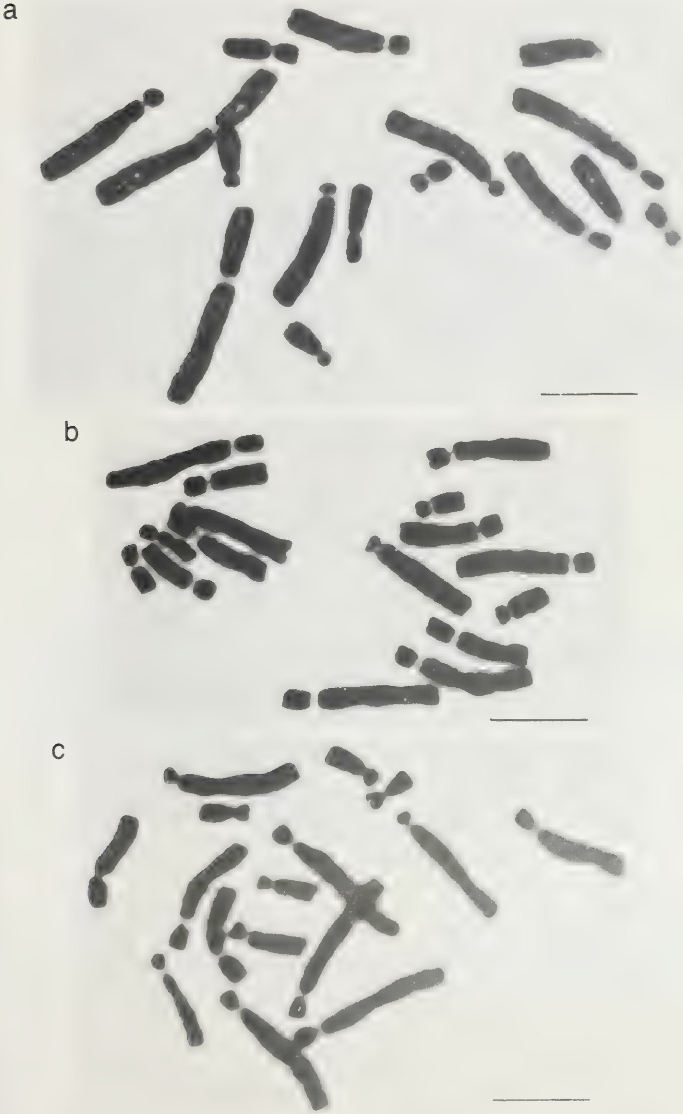

FIG. 8.
a. Mitotic metaphase in the race ST5 of *H. albiflos* [*L*-3]; b. *H. crispus* [*S*-1]; c. *H. strigosus* [*S*-1].

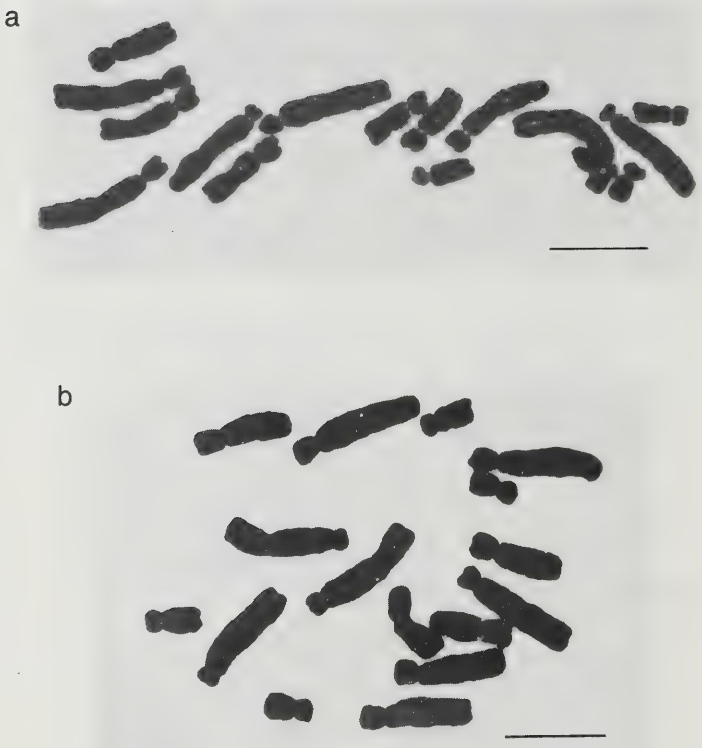

FIG. 9.
a. Mitotic metaphase in *H. barkerae* [*S*-2]; b. *H. namaquensis* [*S*-3].

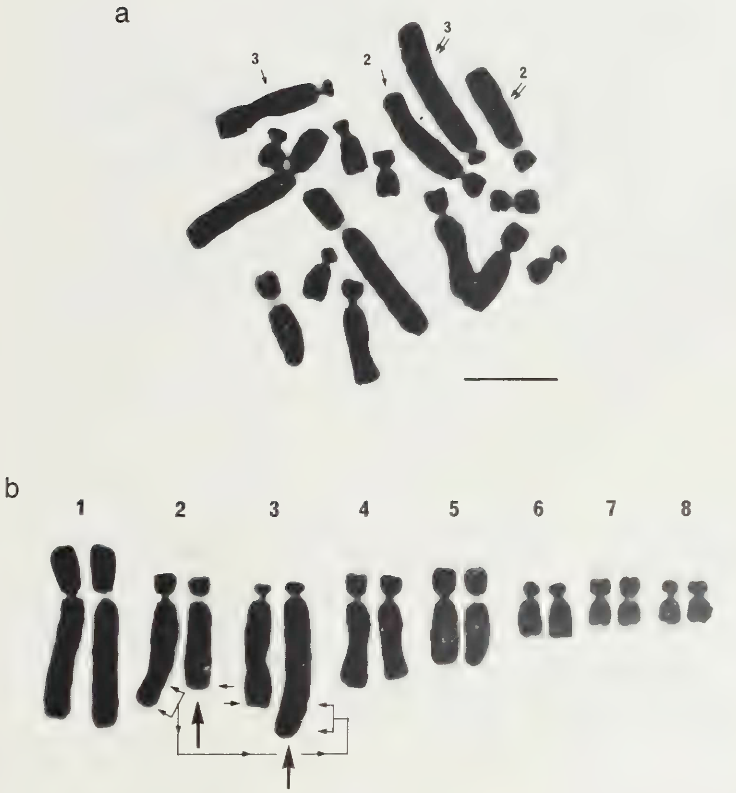

Fig. 10.
a. Mitotic metaphase in the heterozygous plant of *H. canaliculatus* [*L*-1]. The interchanged and the normal homologues, 2 and 3, are indicated by double and single arrows, respectively. b. The reconstructed diploid complement of the heterozygous plant of *H. canaliculatus* (from Fig. 10a). The interchanged chromomes are indicated by the large arrows. The assumed points of breakage and reunion are indicated by the small arrows.

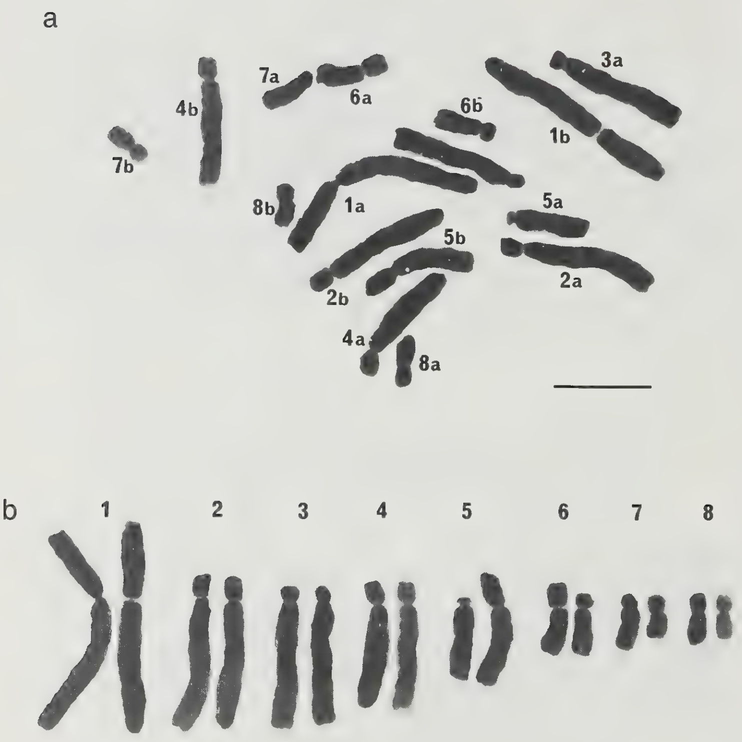

FIG. 11.
a. Mitotic metaphase in the hybrid between the SM5 and the ST5 race of *H. albiflos*. The chromosomes are identified by sequential numbering and by *a* and *b* for race SM5 and ST5, respectively. b. The chromosome complement of the hybrid between the SM5 and the ST5 race of *H. albiflos*, arranged in a linear sequence with the presumed homologous chromosomes paired, SM5 chromosomes left and ST5 chromosomes right.

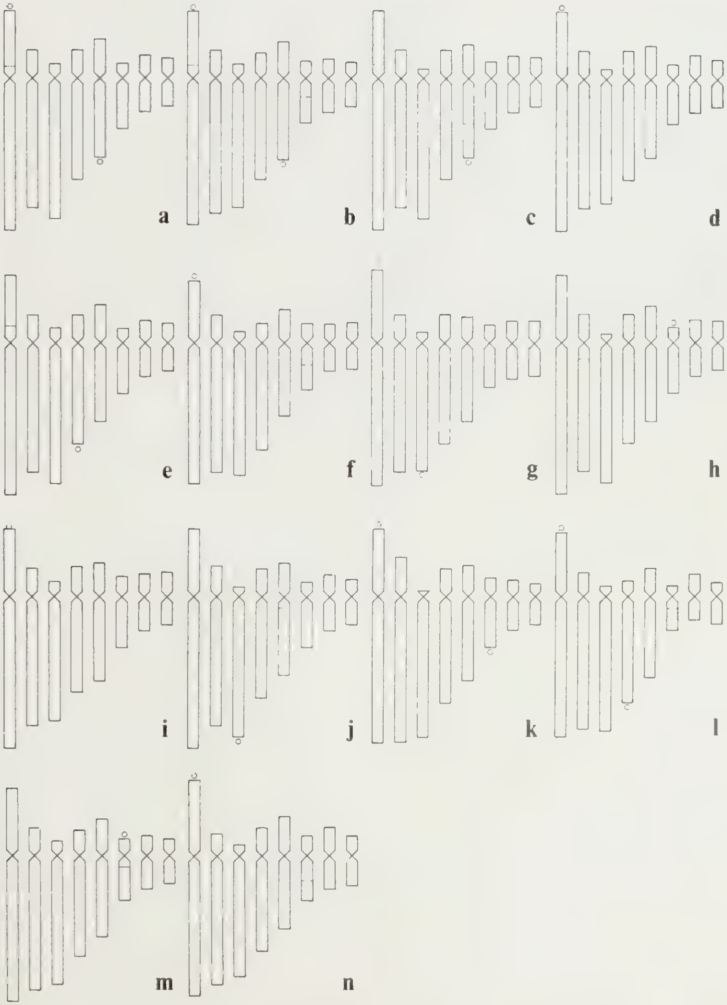

FIG. 12.

Ideograms of the haploid karyotypes of: a. *H. humilis* subsp. *hirsutus*; b. *H. montanus*; c. *H. sanguineus*; d. *H. canaliculatus* (normal karyotype); e. *H. pumilio*; f. *H. lanceifolius*; g. *H. amarylloides* subsp. *polyanthus*; h. *H. amarylloides* subsp. *toximontanus*; i. *H. graniticus*; j. *H. coccineus*; k. *H. unifoliatus*; l. *H. pubescens* subsp. *pubescens*; m. *H. pubescens* subsp. *leipoldtii*; n. *H. albiflos* (race SM5).

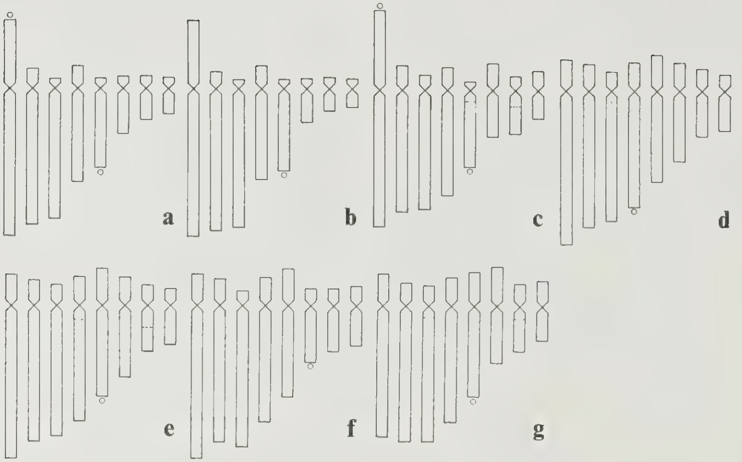

Fig. 13.
Ideograms of the haploid karyotypes of: a. *H. amarylloides* subsp. *amarylloides*, b. *H. pubescens* subsp. *arenicolus*; c. *H. albiflos* (ST5 race); d. *H. crispus*; e. *H. strigosus*; f. *H. barkerae*; g. *H. namaquensis*.

Conclusions

Overall, the cytological data show that chromosome rearrangements have played an important part in speciation in the genus *Haemanthus*.

In Table 5, the species have been listed along the most simple lines of derivation. The *L*-Group on the left is to be considered the most primitive, although it includes some species with distichous bulbs and elaborate spathe valves which appear to be more advanced.

The *S*-Group, which has certain advanced features, has been placed on the right. The derivation point, the unique event of the translocation between chromosomes 1 and 6 (see Figs 1 and 2) and its fixation as a viable and advantageous homozygote, can be placed at any place along the line of the *L*-Group.

A comparison of the systematic conclusions obtained from the cytological data with those independently derived from conventional taxonomic studies, demonstrates good, although not complete, agreement.

It illustrates the value of the two different approaches to the problems of evolution and speciation by reciprocally highlighting and integrating the question of the concept of species as 1) groups of interbreeding individuals and their progeny undergoing constant selective pressure, or 2) groups of morphologically intergrading individuals spread over diverse environmental situations.

The findings of the chromosome analysis confirm the hypothesis that differences between species arise, or rather begin as, differences within species.

They make clear that chromosome rearrangements such as interchanges and inversions are of frequent occurrence in *Haemanthus*.

Those rearrangements which have become established as homozygotes have led to the creation of new karyotypes. Through degrees of genetic isolation and the presence of positive selection for certain characters, this in turn has led to the formation of new species.

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